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Field studies on the spread of African cassava mosaic

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SUMMARY

The spread of African cassava mosaic disease (ACMV) into healthy cassava fields was recorded at weekly intervals. In addition, 21 yellow water traps were placed in one field and the number of whiteflies caught was recorded twice a week. The number of *Bemisia* spp. feeding on cassava was also estimated. The results indicate that the pattern of disease spread is related to the pattern of infestation with *Bemisia*.

Airborne whiteflies carried by the south-west prevailing wind alighted preferentially on cassava plants along the upwind edges (south and west borders) of the plantings. The pattern of incidence of mosaic disease resembled that of whiteflies. Along the SW-NE diagonal, there was a gradient of disease incidence with a maximum at the SW corner block. Similar gradients occurred in three different fields and they were maintained throughout the 6-month study, although gradually flattening with time. There were indications that the reservoirs both of the virus and of the vectors were located some distance upwind from the experimental fields.

INTRODUCTION

African cassava mosaic disease seriously decreases the yield of crops in Africa. It was first reported in 1894 and has since been observed in all parts of East, West and Central Africa and in the adjacent islands (Dubern, 1976). In the Ivory Coast, all cassava (*Manihot esculenta* Crantz.) cultivars show more or less severe symptoms. The causal agent of the disease is a virus, first isolated in East Africa, and named cassava latent virus (Bock & Guthrie, 1977) but now named African cassava mosaic virus (ACMV) by Bock & Woods (1983).

The same pathogen was found in the Ivory Coast (Walter, 1980) and Nigeria (Adejare & Coutts, 1982). The virus is transmissible from cassava to cassava by grafting and by the whitefly *Bemisia tabaci* (Storey & Nichols, 1938; Chant, 1958, Dubern, 1979). It can also be transmitted by inoculation of sap from cassava to *Nicotiana* spp. and is a member of the geminivirus group (Bock, Guthrie & Meredith, 1978; Harrison *et al.*, 1977).

There is comparatively little information on the epidemiology of whitefly transmitted geminiviruses in general (Costa, 1976; Goodman, 1981*a, b*) and on the epidemiology of African cassava mosaic virus (ACMV) in the Ivory Coast in particular (Fauquet & Thouvenel, 1981). Experiments were therefore conducted to study the pattern of virus spread into healthy cassava crops.

MATERIALS AND METHODS

Field surveys

Healthy cassava cuttings of the CB cultivar were obtained from healthy cassava fields at

Toumodi Experimental Station, 200 km to the north of Abidjan (Fauquet & Thouvenel, 1981).

Three plantings of healthy cassava were established at the Experimental Station at Adiopodoumé (coastal area of the Ivory Coast, 20 km west of Abidjan). These plantings were of 0·7 to 1·0 ha divided into blocks of 100 plants (10 rows × 10) and were located in different ecological situations. Field 1 (0·7 ha) was full exposed to the wind and was several hundred m from other cassava plants. Field 2 was surrounded by a wind break, composed of three rows of sugarcane, 2·5 m high. Field 3 was surrounded on three sides by a border containing diseased wild cassava (*Manihot glaziovii*) and was close to a heavily infected cassava field (Plate 1).

Field 1 was planted in February 1982 and infection was recorded at weekly intervals, the diseased plants being removed as soon as they showed symptoms. Fields 2 and 3 were planted in early October 1982 and infection was recorded every 2 wk, when any diseased plants were labelled.

Whitefly surveys

After preliminary studies with a dozen types of insect trap of different colour and shape, a circular yellow water trap of 30 cm diameter, 7 cm high was chosen. Taxonomy of whiteflies is complex and is based on the fourth instar larvae, whose appearance depends on the form of the host plant cuticle on which they develop (Mound, 1963; Mound & Halsey, 1978). Thus although the whiteflies collected from the yellow traps resembled *Bemisia tabaci* several *Bemisia* species may have been included.

In field 2, 21 yellow water traps (Mound, 1962) were located in the centres of several blocks (see Figs 1 and 2 for details). The catches were removed twice a week and the number of whiteflies recorded.

In addition, periodical counts were made of the whiteflies on the five terminal leaves on one shoot tip by holding each leaf by the petiole with two forefingers and gently turning it upside down. As there is a prevailing south-west wind during most of the year, the counts were made along the SW-NE diagonal of a plot.

In further trials, 40 healthy young cassava plants in pots were placed in a uniform grass field (field A) and in a grass field (field B) which also contained volunteer plants (about 1 ha for each field). In field A the potted plants were about 100 m and those in field B were several hundred m away from other cassava.

As a control, potted cassava plants were kept under large insect-proof cages (1·60 m long, 1·00 m high, 0·90 m wide) near the exposed plants. The plants were changed every 3 wk, watered each day, and the number of adult *Bemisia* was assessed periodically. The trial was repeated several times between February and April 1983. In addition, we placed pots of cassava and a yellow water trap on the top of a tower 5 m high and 100 m away from other cassava plantings.

RESULTS

Vector distribution

Fig. 1*a* illustrates the distribution of the catches in Field 2 over a 2-month period. Distribution of the catches is not homogenous throughout the field. More whiteflies were trapped along the south and west borders (an average of 296 and 198 whiteflies per trap respectively) than along the north and east border (138 and 86 whiteflies) or in the centre of the planting (113). There is an increase in the catch from the east to the west along the south border (214 and 423 whiteflies for the SE and SW trap respectively) and from the north to the south along the west border (112 and 423 whiteflies for the NW and SW trap respectively). The south-west corner trap had the highest catch (423) and centre trap the lowest (72).

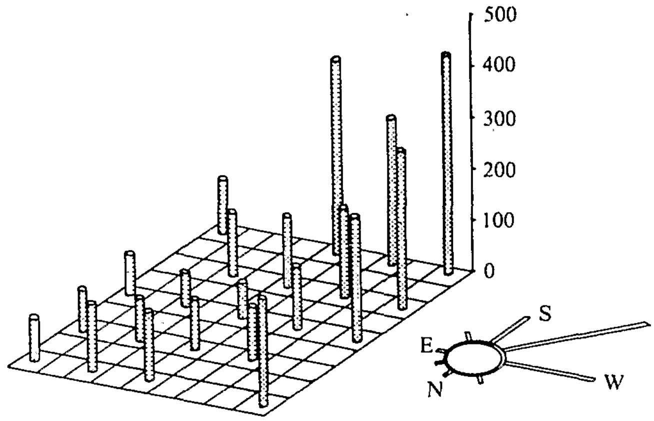

Fig. 1*a*

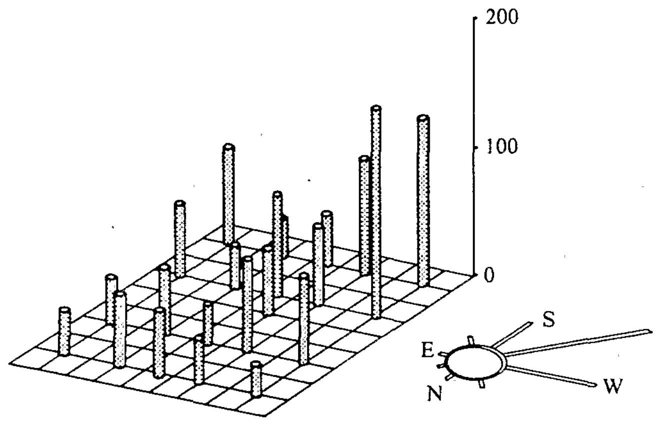

Fig 1*b*

Fig. 1. Distribution of the number of whiteflies caught in yellow water traps in a 0·8 ha cassava field, surrounded by a sugarcane wind-break, during the first and second months of growth (*a*) and during the third month of growth (*b*). On the right side of each graph, the four directions symbol indicates the wind-frequency in each direction.

This pattern of distribution with a pronounced edge effect was repeated for each sampling over the 2-month period. It also occurred when traps were located on bare ground before the time of planting (9 September – 1 October) and when the young plants had new leaves (30 October – 18 November).

So that they were not masked by the growing plants, the traps located in the middle of the block were placed at the intersection of the paths from 26 November to 21 December. Although it was less pronounced than before, Fig. 1*b* indicates there was again an upwind edge effect. Mean catches of 97 and 84 *Bemisia* were obtained for traps on the west and south borders respectively, 54 for centre traps and 51 and 40 whiteflies for traps on the east and north borders respectively.

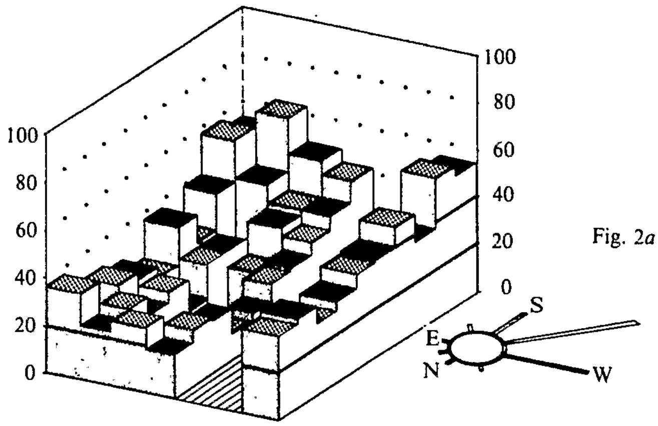

Fig. 2*a*

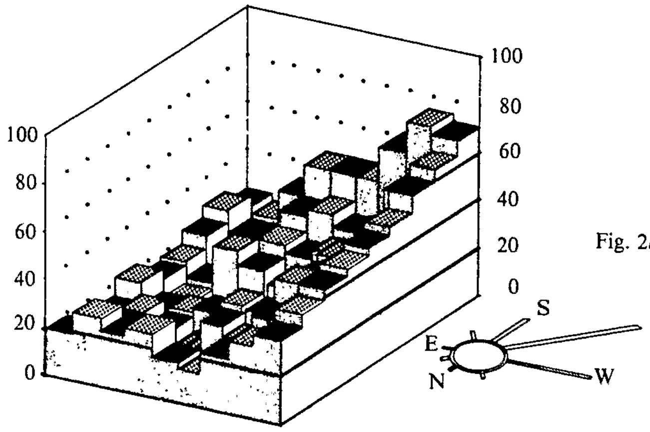

Fig. 2*b*

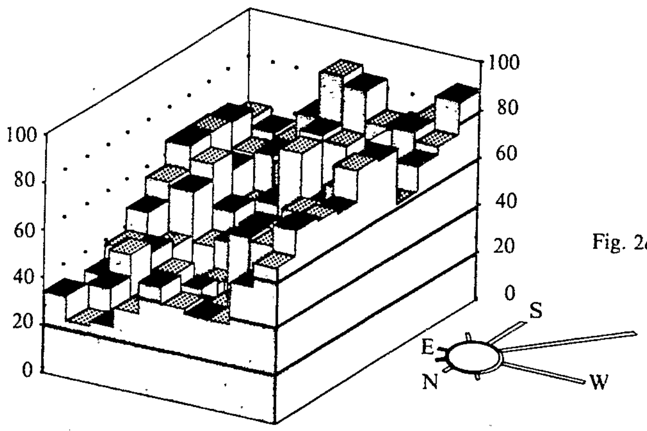

Fig. 2*c*

Fig. 2. Distribution of mosaïc affected plants in a 0·7 ha fully wind exposed cassava field (*a*), in a 0·8 ha cassava field surrounded by a sugarcane wind-break (*b*) and in a 1·0 ha cassava field enclosed along three of its sides by forest (*c*), recorded three months after planting with weekly removal of diseased plants in (*a*) and without removal in (*b*) and (*c*). On the right side of each graph, the four directions symbol indicates the wind frequency in each direction.

Disease incidence

Figs 2*a*, *b* and *c* illustrate the incidence of mosaic disease in the fields after a 3-month period. The mean disease incidence was 31·9%, 27·3% and 47·5% for Fields 1, 2 and 3

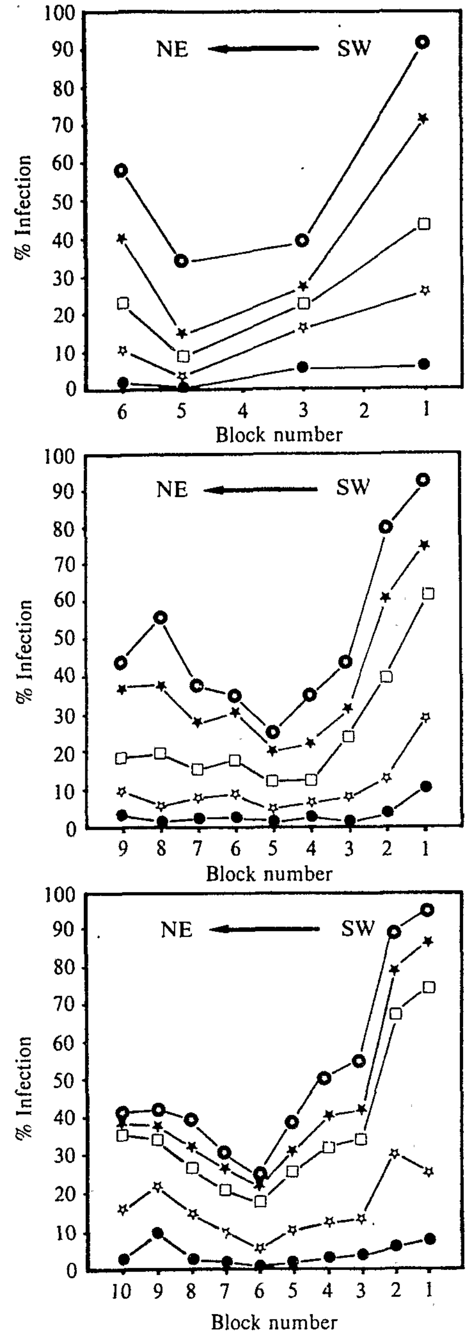

Fig. 3a

Fig. 3b

Fig. 3c

Fig. 3. Development of the gradient of mosaic incidence along the prevailing wind direction of a 0·7 ha fully wind-exposed cassava field (*a*), of a 0·8 ha cassava field surrounded by a sugarcane wind-break (*b*) and in a 1·0 ha cassava field enclosed along three of its sides by forest (*c*), recorded after 1 (●), 2 (☆), 3 (□), 4 (★) and 6 months (○), with removal of diseased plants (*a*) and without removal of diseased plants (*b*) and (*c*). The arrow in each diagram indicates the direction of the prevailing wind.

respectively. The patterns of mosaic incidence show several common features and some differences.

Infection was not homogenous throughout the fields and the wind-exposed south and west had a higher disease incidence than the north and east borders : average incidences for the west, south, north and east borders were respectively 42·2, 52·5, 29 and 33·9% for Field 1; 46·6, 42·8, 20·9, 17·3% for Field 2 and 75·8, 72·4, 40 and 48·9% for Field 3.

Following a SW-NE direction, there is a sharp decrease of disease incidence from the upwind edges, then a plateau around the middle of the fields and eventually an increase towards the downwind edges, steeper for Fields 1 and 3 than for Field 2.

Field 2 (Fig. 2*b*) shows an obvious and regular increase in disease incidence along the south border from west to east and along the west border from north to south, to reach a maximum on the SW corner block. This increase is less regular for Field 3 in either upwind border, although there is also a maximum on the SW corner block, whereas in Field 1 the south border does not have any obvious increase in incidence towards the west.

In Field 3 (Fig. 2*c*) there is no clear focus of disease along the NW edge adjacent to the diseased cassava field, although this field harboured a large whitefly population. There is also no clear cut simple relation between the presence of diseased wild cassava (*M. glaziovii*) and the disease incidence in the nearby parts of Field 3.

Disease gradients

Figs 3*a*, *b* and *c* illustrate the gradients of disease incidence for plantings 1, 2 and 3 at 1 to 6 months, along the SW-NE diagonal. The general pattern of the gradients is apparent as early as the first month, is clearly established by the second month and persists until the sixth month. The gradients have similar features, they show a sharp decrease in disease incidence from the up-wind edges, reach a minimum incidence at the fifth block for Field 2 and at the sixth block for Fields 1 and 3, 50 and 60 m respectively from the SW corner. There is also a slight increase of disease incidence at the NE corner blocks. There was a general tendency for a blurring of the gradients as the max/min ratios decreased with time in each field (Table 1).

Table 1. *Infection ratio between the highest contaminated block and the lowest contaminated block along the main diagonal of the cassava fields*

Field	Months after planting 1	2	3	4	5
1	—	8·0	5·3	4·9	2·8
2	—	6·7	7·1	4·1	4·1
3	12	5·8	4·9	4·1	3·9

Relation between disease incidence and number of Bemisia

Fig. 4 illustrates figures for the SW-NE diagonal of disease incidence, number of transmissions calculated from the multiple infection transformation (Gregory, 1948; Van der Plank, 1963), number of whiteflies counted on cassava tips (average of the two transects on each side of the diagonal) and number of whiteflies caught from 2 August to 23 December 1982.

These curves follow the same general trend, with a decrease from Block 1 (upwind block) and a minimum around the fifth block. Whitefly catches decrease progressively from the first block to the fourth: 423 and 112 (ratio 3·78) and the number of *Bemisia* counted on five tips is 32 on the edge block but only four on the sixth block (ratio 8·0). The number of transmissions ranges from 1·24 per plant in the edge block to 0·1 at the fifth (ratio 12·4), whereas disease incidence ranges from 71% to 10% (ratio 7·1).

Trap plants

In each experiment with potted cassava plants in Fields A and B adult *Bemisia* were observed as early as 1 day after setting out the pots.

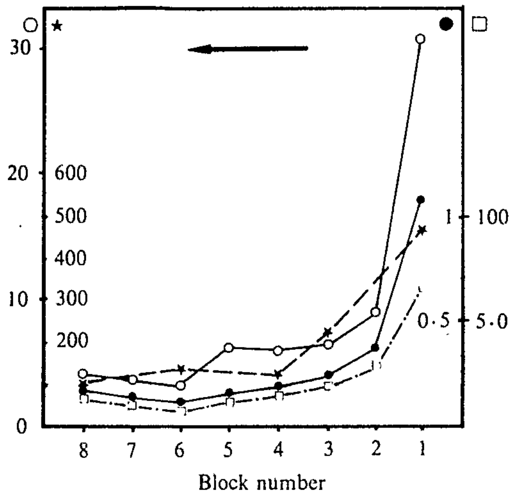

Fig. 4. Percentage of mosaic incidence (□), number of transmissions (●), total number of whiteflies caught in yellow water traps (★), and number of whiteflies counted on cassava tips (O), along the prevailing wind direction of a 0·8 ha cassava field, surrounded by a sugarcane wind-break, after 3 months of growth. The arrow indicates the direction of the prevailing wind.

In one experiment we detected adult *Bemisia* after 2 h. After 2 days an average of two adults per plant was recorded. The number of whiteflies varied considerably from day to day among the plants and the total number of whiteflies on the 40 potted plants fluctuated widely from day to day. In no case were whiteflies observed on nearby potted cassava plants under the large insect proof cages.

After a period of 1 day, *Bemisia* were observed at the top of a 5-m high tower, either on the potted cassava plants, or in the yellow water trap.

DISCUSSION

At the site in the coastal area of the Ivory Coast, there was a rapid spread of cassava mosaic virus into healthy cassava fields in 1982 as in previous years (Fauquet & Thouvenel, 1981). The situation differs from that in Kenya where spread into healthy plantings was slow (2% per year) (Bock & Guthrie, 1977; Bock, 1983). Thus in the coastal area of the Ivory Coast, *Bemisia* is likely to play a major role in the epidemiology of cassava mosaic disease and the study of its movement is critical for the understanding of ACMV epidemiology.

An important finding is the rapid spread of ACMV into Field 1 despite the removal of diseased plants in an attempt to exclude secondary spread. The results, therefore, indicate that there is, over the year, a large influx of viruliferous whiteflies. Within a few miles there are no cassava fields upwind from Fields 1 and 3 and other nearby crops harbour a very limited number of whiteflies in relation to the number caught in water traps. Moreover, young healthy potted cassava plants either on the ground or at the top of a 5-m high tower received *Bemisia* daily although they were at least 100 m away from the nearest source of whiteflies. This suggests that most *Bemisia* entering the crops do not come from a local source but are, on the contrary, carried by the wind from some more distant location. These observations are in line with conclusions from previous work (Thresh, 1971, 1983; Mound, 1973; Leuschner, 1977; Naresh & Nene, 1980) which indicated that *Bemisia* species are typical constituents of the aerial plankton.

Wind direction and intensity have been recognised for a long time as critical for movement of aerial virus vectors (Carter, 1961; Thresh, 1976; Harrison, 1981). The neighbouring diseased cassava field, although harbouring *Bemisia*, did not seem to play a major role in the infestation of the adjoining upwind Field 3. Movement of whiteflies against the wind therefore seemed to be fairly limited. This is consistent with other evidence that wind-borne vectors tend to be carried downwind rather than upwind (Thresh, 1976).

The pattern of whitefly catches in Field 2 resembles the pattern of disease incidence in having a pronounced edge effect on the south and west borders which are upwind. Along the main diagonal the gradients of whitefly catches, of *Bemisia* on the crop, and of disease and transmission incidence show similar trends from maximum at the south-west corner block to minimum around the fifth block.

In general, relations between virus spread and vector populations are complex. For example, the type of plant community, proportion of vectors that are viruliferous and the flight activity of vectors all have a critical influence on the rate of development of epidemics. There is, however, good agreement between the whitefly population and disease incidence in our trials. This is consistent with the knowledge that, along with other geminiviruses (Bock, 1982), the frequency of ACMV infection increases as the size of the vector population increases (Chant, 1958; Dubern, 1979; Seif, 1981). Moreover, Leuschner (1977) established that fluctuations in the *Bemisia* population are reflected in the ACMV incidence in the fields. Similar relations seem to be typical for many persistent and semi-persistent viruses (Thresh, 1976).

The patterns of disease incidence in the three experimental fields show similar pronounced upwind edge-effects and similar decreasing incidence from upwind block to downwind block along the wind-orientated diagonal. Such a distribution of vectors could be explained by the tendency of insects, carried by the wind, to alight preferentially and accumulate on peripheral plants, in our trials especially on the windward borders (Thresh, 1976). This tendency could be reinforced on the windward edge of the sheltered sites (Field 2) because insect deposition and behaviour are further influenced by air turbulence that causes zones of accumulation leeward of windbreaks such as trees, fences, hedges (Lewis, 1966; Lewis, 1969; Lewis & Dibley, 1970).

The general shape of the disease gradients was retained during whole of the 6-month long survey. Although there was an unusual north wind in January and February, it did not much modify the shape of the disease gradients because little infection occurred during these months.

There is a general tendency of such gradients to flatten with time (Van der Plank, 1968; Thresh, 1976). For Field 1, where most secondary spread is excluded the flattening is probably mostly caused by a progressive increase in multiple infection which is greatest in the upwind heavily infected blocks (Gregory, 1948; Van der Plank, 1963). This tendency could be reinforced for Fields 2 and 3 by an increased probability that the plants infected by primary spread from the original source will themselves become infective and so act as secondary foci for further spread (Thresh, 1976).

Much attention has been devoted to gradients of plant diseases in relation to distribution of source of pathogens (Gregory & Read, 1949; Gregory, 1968; Thresh, 1976). However, although ACMV could be transmitted from diseased *M. glaziovii* to *Nicotiana benthamiana* (Walter, 1980) and could be detected in *M. glaziovii* by ELISA (Thouvenel, Fargette, Fauquet & Monsarrat, 1983), we could not relate any clear focus of infection to the position of *M. glaziovii* in Field 3, neither upwind nor downwind. Therefore we think that the role of *M. glaziovii* as a reservoir of ACMV is fairly limited. This conclusion is supported by the observation that *M. glaziovii* harbours only a very small number of whiteflies in relation to the numbers found on cassava or caught in yellow traps. Thus there are several indications that there are no important local sources of virus and that the reservoirs both of the virus and of its vector are located some distance upwind from the field trials.

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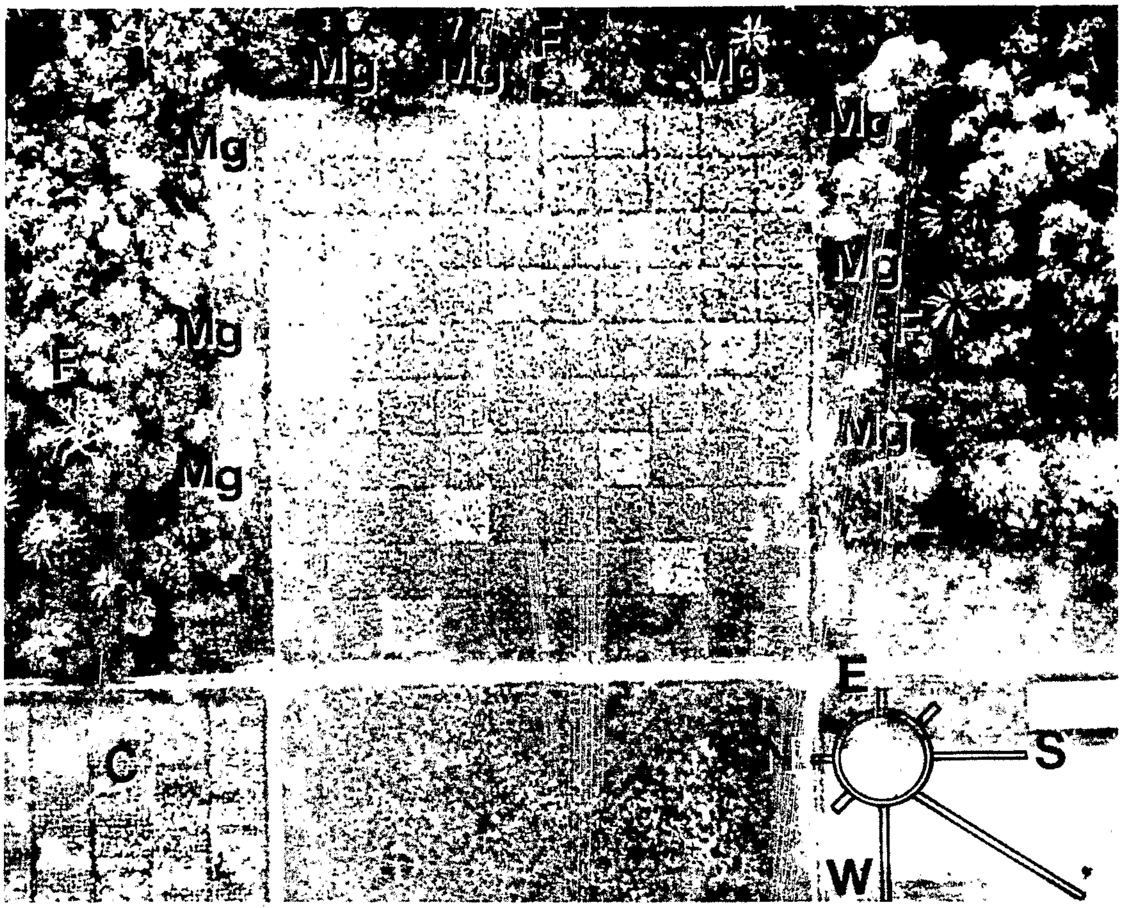
EXPLANATION OF PLATE

Fig. 1. Aerial photograph of the 1·0 ha cassava field surrounded on three of its sides by forest (F). The four directions symbol indicates the wind-frequency in each direction. (C) indicates the location of a collection of cassava clones 100% infected with ACMW. (M.g) indicates the presence of *Manihot glaziovii* 100% infected by ACMW. The paler blocks (one in each row) are planted with a different variety and are not included in the experiment.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